Significance of ungulates in the diet of recently settled wolves in the Mercantour mountains (southeastern France)

Marie-Lazarine Poulle, Lionel Carles, Benoît Lequette

SIGNIFICANCE OF UNGULATES IN THE DIET OF RECENTLY SETTLED WOLVES IN THE MERCANTOUR MOUNTAINS (SOUTHEASTERN FRANCE)

Marie-Lazarine POULLE, Lionel CARLES & Benoît LEQUETTE*

INTRODUCTION

While the wolf (*Canis lupus*) was present in 90 % of the French territory during the 18th century, the human persecution has conducted to the complete extinction of the species in the mid-late 1930s (de Beaufort, 1987). However, in the early 1990s this predator naturally came back in France from Italy where its population has been in numerical and geographical expansion for twenty years (Boitani, 1992). Two wolves were first observed in November 1992 in the Mercantour National Park, close to the Italian border (Houard & Lequette, 1993). During the winter 1994-1995, a pack of eight wolves and another group of two were settled and had reproduced in the Mercantour mountains (Poulle *et al.*, 1995).

These wolves occupied an area characterized by a high diversity and availability of ungulate species. Six wild ungulate species are present: the chamois (*Rupicapra rupicapra*), the moufflon (*Ovis gmelini musimon*), the roe deer (*Capreolus capreolus*) the red deer (*Cervus elaphus*), the wild boar (*Sus scrofa*) and the ibex (*Capra ibex*). Furthermore, large flocks of sheep (*Ovis aries*), some goats (*Capra hircus*) and horses (*Equus caballus*) and some herds of cows (*Bos taurus*) graze in the mountain pastures. Before the natural return of the wolf, the area had been free of ungulate predator for over fifty years.

Wolf predation on domestic and game species led to a strong opposition to this predator from shepherds and some hunters who claim its full withdrawal from the mountains. Although the wolf is a fully protected species in France, it appears that its management is strongly conditioned by public opinion, as observed in Spain (Blanco *et al.*, 1992) and Italy (Boitani, 1992). At a local, national or European scale, the acceptance of this predator depends on several actions as public information campaigns, damage prevention and payment and game management (including wild ungulate reintroduction projects). In order to be correctly organized, all these actions need data about wolf predation on ungulate species.

In this context, the aim of this paper is to provide the first data on the occurrence of wild and domestic ungulate in the diet of wolves newly established in France.

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STUDY AREA

The study only concerned the diet of the main pack present during 1994-95 in the Mercantour because the data collected on the second pack was too small to be included in the analysis. Wolf scats were collected from April 1994 to March 1995 in a 280 km^2 mountainous study area of which 48 % (133 km^2) lays within the core area of the Mercantour National Park (Maritime Alps, Fig. 1). The altitude ranges from 700 m to 2,500 m a.s.l. About 34 % of the area is covered with pines, larches and mixed forest. Alpine meadows and pasture cover 66 % of the area. There are very few human settlements in the area. Feral dogs do not exist in the core area of the Park and free-ranging dogs are extremely rare. In the buffer zone of the National Park, some livestock guarding dogs, shepherd dogs and dogs belonging to tourists are present during summer. During the study period, the local wolf pack numbered 8 individuals in early winter according to conservative estimates by snow tracking and direct observations.

The six wild ungulate species are present within or in the periphery of the study area. As a consequence of the prohibition of hunting within the core area of the park, the chamois is abundant (about 1,000/100 km^2). A population of 300 moufflons is present (about 100/100 km^2) following introduction by the local hunting association in the 1950's. The roe deer and the wild boar are also present, their populations are in expansion but their size is unknown. The red deer has been reintroduced in the 1970s and its main population (250 individuals) is located in periphery of the study area. About 200 ibex are present from May to October coming from a larger Italian population. Livestock mainly includes sheep with large flocks of 1,500 to 2,000 animals adding up to a total amount of about 10,000 head (about 3,000/100 km^2). Some cows and horses also graze from June to October in this area.

MATERIAL AND METHODS

SCAT COLLECTION AND LABORATORY PROCEDURE

Analytical procedure followed that described by Ciucci *et al.* (1996). Wolf scats were collected along paths, trails, and dirt roads according to an opportunistic sampling (Fritts & Mech, 1981) and by following wolf tracks in the snow. Age of deposition was estimated on the basis of the time elapsed from the last scat-trail coverage (maximum 2-5 weeks depending on the scat-trail), the scat appearance, exposure of deposition site, and weather conditions. In order to discriminate scats which could be confidently attributed to wolf from those that might belong to dog or fox, we adopted a multiple criteria and conservative approach similar to that described by Ciucci (1994). We considered the proximity of wolf tracks, the size of the scat, its location and its smell. About 10 % of the scats collected each month were discarded in order to keep only scats considered as wolf's.

Scats were collected in plastic bags, labelled and stored in a freezer (– 30 °C) for later analysis. Prior to treatment, each scat was oven-dried (70 °C for 48 hours). Micro- and macro-components were separated by thorough washing in a sieve (0.5 mm mesh). Macro-components were hand-sorted by food item (hairs, bones, seeds, etc.).

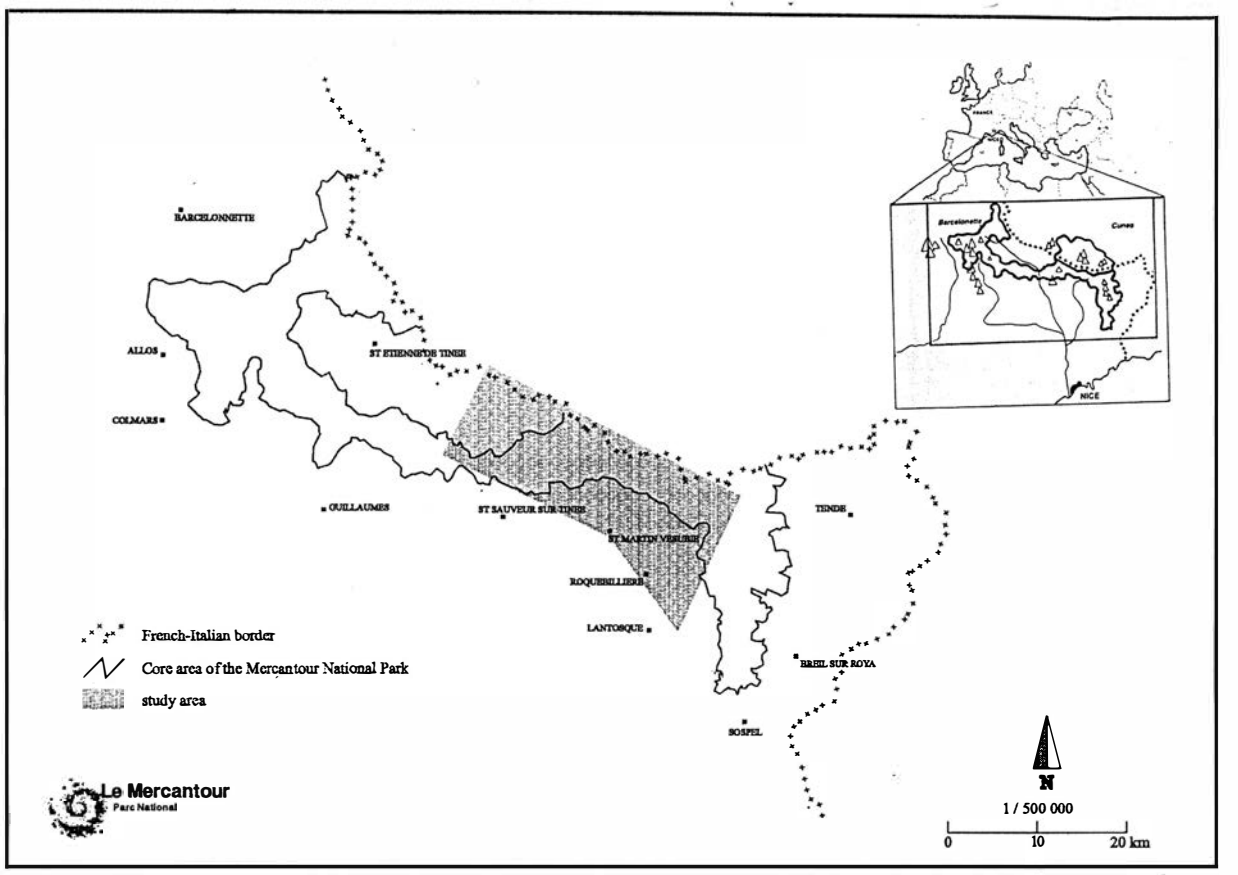

Figure 1. — Location of the study area in France and in the Mercantour.

For species identification hairs of different mammal species were first separated by macroscopic analysis of colour and length. Then, the microscopic examination of the medulla pattern allowed to differentiate i) ungulates hair from those of carnivores, rodents or lagomorphs and ii) wild ungulates hair versus domestic ones. Except for wild boar hair which could be identified by a macroscopical examination (Brunner & Coman, 1974; Keller, 1981), the specific identification of wild ungulate hair was made according to the microscopic examination of the cuticular pattern near the base and in some cases by analysing the cross-section through the plate method (Brunner & Coman, 1974). Comparison was made to a hair collection of mammal species collected locally, and to reference manuals by Brunner & Coman (1974), Keller (1981), Debrot *et al.* (1982) and Teerink (1991).

The accuracy of trained observers (M.-L. P. and L. C.) in identifying wild ungulate hairs was assessed through a blind test (Fritts & Mech, 1981; Ciucci *et al.*, 1996) on a sample of 100 guard hairs of the back, the flank and the abdomen of chamois, moufflon, roe deer and red deer. Reported accuracy in the examination of cuticula pattern was 94 % and 96 % respectively for the two observers. The 6 % and 4 % errors occurred when the hair were too fine or their base missing. For that reason we decided that when we encountered at least one of these two situations the identification at the species level was not possible. In this case the food items were grouped as "unidentified wild ungulates".

Four periods were distinguished for the analysis:

— April-June (spring) which covers the breeding period of wild ungulates;

— July-September (summer), grazing period in which large flocks of domestic ungulates are present;

— October-December (autumn), end of the grazing period and first snow fall;

— January-March (winter), snow cover.

Method of scat analysis

Data was tabulated as percentage of occurrence (Lockie, 1959). Although it is not without limitations, this method was chosen because i) it is the most commonly used, ii) it quickly provides qualitative description of the diet and iii) it is the less laborious and time consuming one to apply (Ciucci *et al.*, 1996). The frequency with which each food item occurs is expressed as a percentage of the total number of occurrences of all food items (relative frequency), rather than a percentage of the total number of scats (absolute frequency) because the former measure is believed to be more meaningful in terms of diet composition (Ciucci *et al.*, 1996). The frequency method mainly suffers from the surface to volume ratio bias of varying prey sizes (Floyd *et al.*, 1978; Reynolds & Aebischer, 1991; Ciucci *et al.*, 1996). However this bias is reduced in the present analysis because only preys of similar size (large wild ungulates like moufflon, chamois, sheep) are taken into account. As Ciucci *et al.* (1996) proposed, remains whose proportions in a scat were < 3 % were not considered in the analysis in order to reduce the bias occurring when food items contributing different amounts to a scat's volume are equated by frequency. Statistical significance of the differences in the consumption of ungulate species was assessed using a χ^2-test on frequency of occurrence data. The marginal totals in the contingency table were the total number of occurrences.

RESULTS

A total of 236 scats were collected from April 1994 to March 1995. Among these, 21 % were collected in spring, 21 % in summer, 29 % in autumn and 29 % in winter (Fig. 2). The seasonal distribution of the sample was homogeneous (χ^2 = 6.14, $p > 0.05$). The number of scats collected each month averaged 19.6 ± 9.39 (min. = 8, max. = 32).

Only 266 different food items were identified overall (excluding graminaceae present in 18 % of the scats but considered as a purgative), showing that most of the scats only contained a single food item. From the 236 scats analysed, 229 (97 %) contained ungulate remains. The 7 scats which did not were composed of remains of rodents (voles Microtidae and marmots, *Marmota marmota*), hares (*Lepus* sp.), amphibians and pine-cones. From the total number of occurrences 91 % were ungulate remains (wild and domestic pooled) during the whole year and respectively 94 %, 87 %, 87 %, and 94 % in spring, summer, autumn and winter. This percentage of ungulate remains was significantly higher in spring and winter than in summer and autumn (χ^2 = 4.04, $p < 0.05$).

During the whole grazing period (July-December) domestic ungulates were present in 33 % of the 118 scats collected. The only domestic ungulate found in the scats was sheep. Its remains did not occur in scats collected in spring and their occurrence relative to the total number of ungulate remains was very low in winter (4 %), whereas it was respectively 50 % and 22 % in summer and autumn (Fig. 2). This percentage was significantly higher in summer than in autumn (χ^2 = 9.32, $p < 0.01$, Fig. 2).

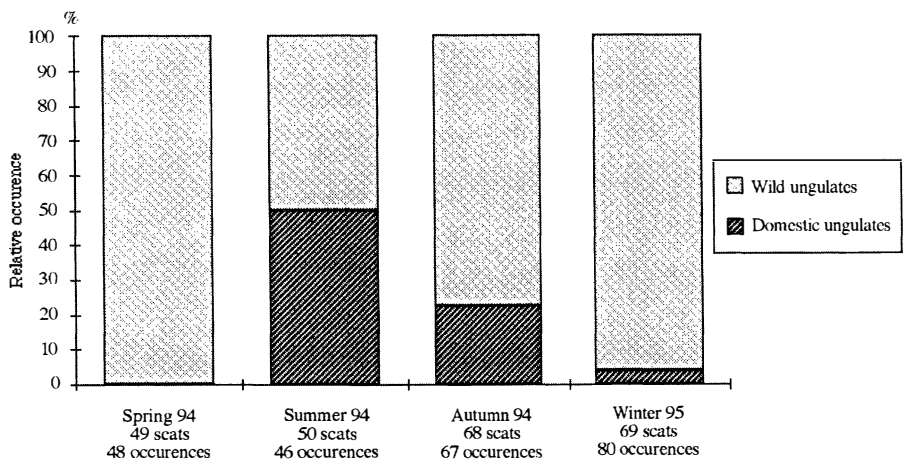

Figure 2. — Occurrence of wild and domestic ungulates relative to the total occurrence of ungulates in wolf scats collected from April 1994 to March 1995 in the Mercantour mountains.

Wild ungulate remains occurred in 80 % of the scats analysed. Their occurrence relative to the total number of ungulate occurrences ranged from 50 %

in summer to 100 % in spring (Fig. 2). Of the 200 wild ungulate items analysed, 148 were identified at the species level. The hair of only three species were found: moufflon, chamois and wild boar. Wild boar hair was found in scats including also moufflon remains (11 cases during winter) or alone (1 case in autumn). Respectively 3 % and 16 % of the total number of identified wild ungulate remains in autumn and winter were wild boar (Fig. 3). The relative occurrence of moufflon ranged from 29 % to 68 % according to the season while those of chamois ranged from 26 % to 71 % (Fig. 3). The occurrence of moufflon remains relative to the total number of identified wild ungulate remains was almost twice those of chamois in spring, autumn and winter (Fig. 3). As these occurrences did not vary significantly between these three periods ($\chi^2 = 0.8$, $p > 0.05$) they were pooled. The occurrence of moufflon relative to the total number of identified wild ungulate remains was significantly lower in summer than in the rest of the year (with Yate's correction $\chi^2 = 7.28$, $p < 0.01$). During this season, the relative occurrence of the chamois is more than twice that of the moufflon (Fig. 3).

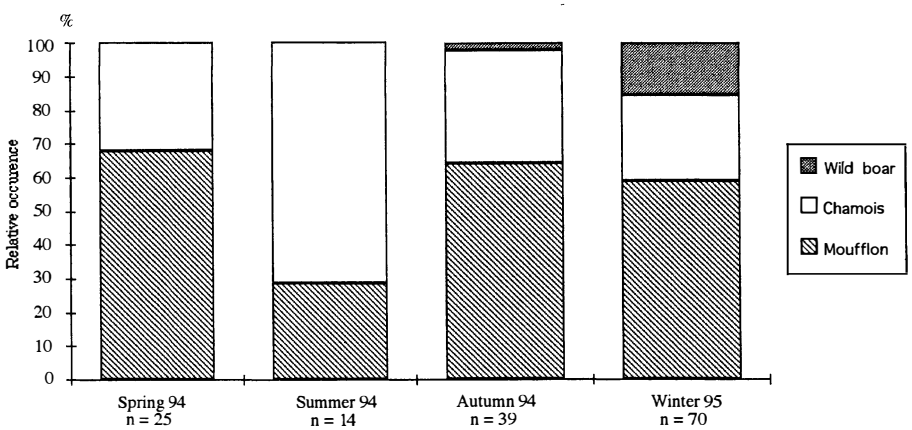

Figure 3. — Occurrence of wild boar, chamois and moufflon relative to the total occurrence of identified wild ungulates remains in wolf scats collected from April 1994 to March 1995 in the Mercantour mountains.

DISCUSSION

Numerous studies conducted in North America (Pimlott, 1967, 1975; Potvin & Jolicœur, 1988), in Eastern Europe (Reig & Jedrzejewski, 1988) and in Mediterranean area (Tellería & Sáez-Royuela, 1989; Cuesta *et al.*, 1991; Meriggi *et al.*, 1996) have shown that the wolf feeds mostly on ungulates throughout the year. The significance of fruits, rubbish, and small and medium mammals reported in some southern European areas where large herbivores are not abundant (Boitani, 1983; Reig *et al.*, 1985; Meriggi *et al.*, 1991) has been related to impoverished ecological situations (Meriggi *et al.*, 1991; Mattioli *et al.*, 1995). In

our study area which is characterized by a rich ungulates community (6 wild ungulate species and 4 domestic ones), it was therefore supposed the wolves could primarily rely on ungulates for prey. The frequency of occurrence of pooled wild and domestic ungulates (87 %-94 %) was higher (and inversely the occurrence of other food categories lower) in the Mercantour than Meriggi & Lovari (1996) reported for studies of wolf diet conducted in Italy (mean occurrence 72,9 %, n = 10) and Spain (mean occurrence 70,1 %, n = 5) in areas where large herbivores are less abundant. This observation is consistent with the hypothesis of Meriggi *et al.* (1996) that wolf prefers large prey and that the abundance of this large prey affects the use of other food categories and diet breadth.

Livestock predation by wolves is frequently observed in Southern Europe and concerns calves, foals, goats or sheep (Braña *et al.*, 1982; Salvador & Abad, 1987; Tellería & Sáez-Royuela, 1989; Brangi *et al.*, 1991; Cuesta *et al.*, 1991; Blanco *et al.*, 1992). In our study area, the availability of goats, calves and foals is low and, furthermore, calves and foals are included in herds which exert active defence against predators (Meriggi *et al.*, 1991). The only domestic ungulate remains we found were those of sheep. This is not surprising regarding to the local abundance and accessibility of this species. The lack of protection of free-ranging sheep, which represents the most important type of livestock in the Mercantour mountains, makes them prone to be the main target of wolf predation on livestock as observed in several regions in Spain (Braña *et al.*, 1982; Ragni *et al.*, 1985; Blanco *et al.*, 1992) and Italy (Meriggi *et al.*, 1991; Fico *et al.*, 1993; Meriggi & Lovari, 1996). In our study area wolves fed more upon livestock in summer than in autumn (Fig. 2) suggesting that predation on sheep was partially dependent on their abundance.

Red deer, roe deer and wild boar are preys for the wolf in several regions of Spain (Braña *et al.*, 1982; Salvador & Abad, 1987; Guitian & Bermejo, 1989; Vignon, 1995) and Italy (Meriggi *et al.*, 1991). In our study area these three species are present but relatively scarce and this can perhaps explain why red deer and roe deer did not occur in the scats analysed and wild boar only scarcely. Moufflon and chamois, which are the most abundant wild ungulates, made up the bulk of the wolf's diet. The relative occurrence of moufflon was almost twice that of chamois from autumn to spring despite the fact that moufflon is ten time less abundant than chamois in the study area. Thus, as in most studies of the wolf's diet, we found a non-random representation of the available food in the observed diet, which reveals a prey selectivity (Chesson, 1978).

Differences in the accessibility and/or vulnerability of the two species could explain the selectivity of moufflon by the wolf. As enhanced by Cowan (1947) and Bibikov (1982 in Huggard, 1993) the complex topography in the mountains results in either a quick kill by the wolves or a quick escape by the prey. Furthermore, snow depth can alter selectivity in reducing the ability of preys to escape (Mech *et al.*, 1987). The chamois is an alpine species very well adapted to snow conditions and to the topography of the alpine valleys of the study area. It can be assumed that it is not an easy prey to catch for the wolf in reason of its ability to climb sheer cliffs quickly. In southern Europe this species has been rarely taken by wolf despite its local abundance (Meriggi & Lovari, 1996). On the opposite, the moufflon, originated from mountains of Corsica and Sardinia and introduced in this part of the Alps forty years ago, is a species very sensitive to important snow levels. It cannot escape easily when the snow depth is important. Furthermore, the moufflon is a more gregarious species than the chamois, especially during winter.

During this period, the chamois is more often encountered randomly while a large part of the moufflon population occurs in herds that are predictably associated with good habitat patches. In these conditions, wolves can often travel from one predictable herd "territory" to another and hunt intensively in these areas (Huggard, 1993). Furthermore, during the snow cover period the moufflon tends to stay in lower altitudes than the chamois, nearer to valley bottoms where random encounters with wolves are more likely. These diverse explanations for moufflon selection by the wolf are supported by the greater consumption of this species by the wolf observed during the snow cover period (autumn to spring, Fig. 3). Furthermore, the anti predator behaviour of the moufflon is likely to be less efficient than that of the chamois (Lequette *et al.*, unpublished data), as the original population of moufflon has never been in contact with the wolf. The selectivity of moufflon by the wolf during spring can be also explained by another factor: the breeding period. Young ungulates are often selected by wolves because they are generally slower, less dangerous and inexperienced with predators (Mech, 1970). The moufflon is the first ungulate species to breed in the Mercantour, births occur more than one month before those of the chamois and deer. A large proportion of moufflon consumption during spring probably concerns young of the year. During summer, young of other wild ungulate species are available, the ability of the moufflon to escape is similar to that of the chamois and the two species occupy the same habitat. This decrease of the moufflon's vulnerability is supported by the lower consumption of this species during this season (Fig. 3).

As enhanced by Meriggi *et al.* (1996) according to optimal foraging and optimal diet theories, wolves should select domestic rather than wild ungulates because of their clumped distribution in a few known pasture areas, their low ability to recognize and avoid predators and their low escape effectiveness. However, we observed that in the Mercantour the consumption of wild ungulates by wolves exceeds or equals that of the domestic ungulates during the grazing period (Fig. 2) despite the fact that sheep are almost 2.5 times more abundant than wild ungulates and despite their lack of protection. Thus, our data are in accordance with Italian and Iberian studies that suggest that wild ungulates are preferred to livestock (Meriggi & Lovari, 1996). Meriggi *et al.* (1996) suggested that the risk for the wolf of being disturbed or killed by man make domestic prey less profitable than wild ones because the wolves have a high probability of being unable to exploit the kill entirely.

It is sometimes assumed that livestock is an alternative prey where wild ungulates are not very abundant (Tellería & Sáez-Royuela, 1989; Brangi *et al.*, 1991). Wolf predation on livestock is supposed to rarely occur in areas where wild herbivorous guilds are characterized by high diversity and richness (Fritts & Mech, 1981; Meriggi *et al.*, 1996). According to this assumption, livestock depredation should be rare in our study area. However, 33 wolf attacks on flocks, resulting in 103 victims, occurred in this area during the 1995 grazing period (Dahier, 1995). Although wolf scats might contain carrion remains (Ciucci, 1994) the significance of damage in our area suggests that sheep consumption by wolves probably refers essentially to predation. We observed that the absolute frequency of livestock in the wolf's diet during the whole grazing period was 33 %, which is similar to the mean occurrence observed in Italy (35,9 %, n = 10) and Spain (34 %, n = 5, Meriggi & Lovari, 1996). Furthermore, during the summer 1994, the main Mercantour pack consumed as many domestic ungulates as wild ones despite the presence of six wild ungulate species on their territory. Similarly, Patalano &

Lovari (1993) found wolves preying on domestic ungulates in central Italy despite the presence of four wild ungulate species.

Our data show that predation on domestic ungulates is not necessarily rare in areas characterized by a rich and diverse herbivorous guild. As livestock predation seems to be mainly influenced by local breeding practice (Braña *et al.*, 1982; Meriggi *et al.*, 1991; Blanco *et al.*, 1992), in order to be successful, wild herbivore reintroduction projects determined to reduce predation on livestock (Meriggi & Lovari, 1996) must be linked to efficient measure to discourage wolves from taking domestic animals (use of livestock guarding dogs, nocturnal housing, presence of a shepherd, etc.).

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SUMMARY

In the early 1990s the wolf (*Canis lupus*) settled in the Mercantour's mountains, southeastern France. Its predation on domestic and game species prompted a strong opposition from part of the local residents. In this context, it appeared of prime importance to collect data on the occurrence of ungulates in the wolf's diet. The diet was determined through the analysis of 236 scats collected from April 1994 to March 1995 in a 280 km^2 mountainous study area where a pack of 8 wolves was settled. The chamois (*Rupicapra rupicapra*) is abundant (about 1,000/100 km^2) in this area and a population of 300 moufflons (*Ovis gmelini*) was present. There are also small populations of roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), ibex (*Capra ibex*) and wild boar (*Sus scrofa*). Concerning livestock, 10,000 sheep (*Ovis aries*), some cows (*Bos taurus*), goats (*Capra hircus*) and horses (*Equus caballus*) graze from June to October in the study area. Ungulates (wild and domestic pooled) made up the bulk of the wolf's diet, occurring in 97 % of the scats analysed. Their relative occurrence varied from 94 % in winter and spring to 87 % in summer and autumn. Wild ungulates remains, mainly those of moufflons and chamois, occurred in 80 % of the scats analysed. In summer, the chamois occurrence relative to wild ungulates was more than twice that of the moufflon (71 % vs 29 %). Conversely, the relative occurrence of the moufflon was almost twice that of the chamois in spring (68 % vs 32 %), autumn (64 % vs 33 %) and winter (59 % vs 26 %) despite the fact that moufflons were ten times less abundant than chamois. The seasonal selectivity of moufflons by wolves was probably related to the fact that the moufflon i) cannot escape easily when the

snow depth is important, ii) occurs in herds that are predictably associated with good habitat patches during winter, iii) tends to stay in lower altitude than the chamois from autumn to spring and iv) is the first ungulate species to breed in the Mercantour. Concerning domestic ungulates, free ranging sheep were the main target of wolf predation on livestock because of their local abundance and accessibility. The sheep's occurrence relative to the total ungulate's one was 50 % in summer (main grazing period) and 22 % in autumn. Wild ungulates were preferred to livestock. However, our data show that, when prevention methods are lacking, the predation on domestic ungulates is not necessarily rare in areas characterized by a rich and diverse wild ungulate guild.

RÉSUMÉ

Le Loup (*Canis lupus*) s'est établi au début des années 90 dans le massif du Mercantour, au sud-est de la France. La prédation qu'il exerce sur le cheptel domestique et sur les espèces gibier suscite de vives réactions de rejet auprès d'une partie de la population locale. Dans ce contexte, il est apparu primordial d'évaluer la part des ongulés dans le régime alimentaire du loup. Cette estimation a été effectuée à partir de l'analyse de 236 fèces récoltées d'avril 1994 à mars 1995 sur un terrain d'étude de 280 km^2 fréquenté par une meute de 8 loups. Le chamois (*Rupicapra rupicapra*) est abondant sur ce terrain d'étude (environ 1 000/100 km^2) et 300 mouflons (*Ovis gmellini*) étaient présents. On note également la présence de petites populations de chevreuil (*Capreolus capreolus*), cerf (*Cervus elaphus*), bouquetin (*Capra ibex*) et sanglier (*Sus scrofa*). De plus, environ 10 000 moutons (*Ovis aries*) sont présents en alpage du printemps à l'automne dans la zone d'étude. Les ongulés (sauvages et domestiques confondus) constituent la base du régime alimentaire des loups. Ils sont présents dans 97 % des fèces analysées. Leur fréquence relative d'occurrence varie de 94 % en hiver et au printemps à 87 % en été et en automne. Des restes d'ongulés sauvages, essentiellement de chamois et mouflon, ont été trouvés dans 80 % des fèces analysées. En été, la fréquence relative d'occurrence du chamois, par rapport à l'ensemble des ongulés sauvages, a été plus du double de celle du mouflon (71 % contre 29 %). À l'inverse, la fréquence relative d'occurrence du mouflon a été près du double de celle du chamois au printemps (68 % contre 32 %), en automne (64 % contre 33 %) et en hiver (59 % contre 26 %), bien que le mouflon soit dix fois moins abondant que le chamois. La sélection exercée par le loup à l'égard du mouflon durant ces saisons est probablement due au fait que le mouflon : i) a des difficultés à se déplacer quand l'épaisseur de neige est importante, ii) est grégaire et inféodé à quelques lieux privilégiés et prédictibles durant l'hiver, iii) a tendance à se cantonner à de plus basses altitudes que le chamois durant toute la période hivernale et iv) a une période de mise-bas très précoce par rapport aux autres ongulés sauvages présents dans le Mercantour. En ce qui concerne les ongulés domestiques, le mouton est la principale victime des attaques de loup en raison de son abondance relative et de sa vulnérabilité. Il représente 50 % et 22 % du total des occurrences d'ongulés en été et automne respectivement. Les ongulés sauvages sont préférés aux ongulés domestiques mais nos données montrent que, lorsque la surveillance des troupeaux n'est pas adaptée à la présence du loup, la prédation sur les ongulés domestiques n'est pas nécessairement rare dans les régions caractérisées par une communauté d'ongulés sauvages riche et diverse.

REFERENCES

BEAUFORT (DE), F. (1987). — *Le loup en France : éléments d'écologie historique.* Encyclopédie des mammifères de France, S.F.E.P.M., Paris.

BLANCO, J.-C., REIG, S. & CUESTA (DE LA), L. (1992). — Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation*, 60: 73-80.

BOITANI, L. (1983). — Wolf and dog competition in Italy. *Acta Zoologica Fennica*, 174: 259-264.

BOITANI, L. (1992). — Wolf research and conservation in Italy. *Biological Conservation*, 61: 125-132.

BRAÑA, F., CAMPO (DEL), J.C. & PALOMERO, G. (1982). — Le loup au versant nord de la Cordillière Cantabrique. *Acta Biologica Montana*, 1 : 33-52.

BRANGI, A., ROSA, P. & MERIGGI, A. (1991). — Predation by wolves (*Canis lupus* L.) on wild and domestic ungulates in northern Italy. pp. 541-543. *In*: Spitz, F., Janeau, G., Gonzales, G. & Aulagnier, S. (eds). Proceedings of the *"Ongulés / Ungulates 91" conference.* S.F.P.E.M, Paris & IRGM, Toulouse.

BRUNNER, H. & COMAN, B.J. (1974). — *The identification of mammalian hair.* Inkata Press, Melbourne.

CHESSON, J. (1978). — Measuring preference in selective predation. *Ecology*, 59: 211-215.

CIUCCI, P. (1994). — *Movimenti, attività e risorse del lupo* (Canis lupus) *in due aree dell'Appennino centro-settentrionale.* Ph.D. Thesis, University of Roma "La Sapienza", Roma, Italy.

CIUCCI, P., BOITANI, L., PELLICCIONI, E.R., ROCCO, M. & GUY, I. (1996). — A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus. Wildlife Biology*, 2: 37-48.

COWAN, I.M. (1947). — The timber wolf in the Rocky Mountain national parks of Canada. *Canadian Journal of Resource*, 25: 139-174.

CUESTA, L., BARCENA, F., PALACIOS, F.& REIG, S. (1991). — The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia*, 55: 239-254.

DAHIER, T. (1995). — *Constats de dommages sur troupeaux domestiques 1995.* Parc National du Mercantour. Rapport interne.

DEBROT, S., FIVAZ, G., MERMOD, C.& WEBER, J. M. (1982). — *Atlas des poils de mammifères d'Europe.* Université de Neuchâtel, Neuchâtel, Switzerland.

FICO, R., MOROSETTI, G. & GIOVANNINI, A. (1993). — The impact of predators on livestock in the Abruzzo region of Italy. *Revue Scientifique et Technique, Office International Epizooties*, 12: 39-50.

FLOYD, T., MECH, L.D. & JORDAN, P.A. (1978). — Relating wolf scat content to prey consumed. *Journal of Wildlife Management*, 42: 528-532.

FRITTS, S.H. & MECH, L.D. (1981). — Dynamics, movements and feeding ecology of a newly protected wolf population in northeastern Minnesota. *Wildlife Monograph*, 80.

GUITIAN, J. & BERMEJO, T. (1989). — Nota sobre dietas de carnívoros e índices de abundancia en una reserva de caza del norte de España. *Doñana, Acta Vertebrata*, 16: 319-323.

HOUARD, T. & LEQUETTE, B. (1993). — Le retour des loups dans le Mercantour. *Riviéra Scientifique*, janvier 1994 : 61-66.

HUGGARD, D.J. (1993). — Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology*, 71: 130-139.

KELLER, A. (1981). — Détermination des mammifères de la Suisse par leur pelage: V. Carnivora, VI. Artiodactyla. *Revue Suisse de Zoologie*, 88: 803-820.

LOCKIE, J.D. (1959). — The estimation of the food of the foxes. *Journal of Wildlife Management*, 23: 224-227.

MATTIOLI, L., APOLLONIO, M., MAZZARONE, V. & CENTOFANTI, E. (1995). — Wolf food habits and wild ungulates availability in the Foreste Casentini National Park, Italy. *Acta Theriologica*, 40: 387-402.

MECH, L.D. (1970). — The wolf: ecology and behaviour of an endangered species. The Natural History Press, Garden City, N.Y.

MECH, L.D., MCROBERTS, R.E., PETERSON, R. O. & PAGE, R. E. (1987). — Relationship of deer and moose populations to previous winters' snow. *Journal of Animal Ecology*, 56: 615-627.

MERIGGI, A., ROSA, P., BRANGI, A. & MATTEUCCI, C. (1991). — Habitat use and diet of the wolf in northern Italy. *Acta Theriologica*, 36: 141-151.

MERIGGI, A., BRANGI, A., MATTEUCCI, C. & SACCHI, O. (1996). — The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography*, 19: 287-295.

MERIGGI, A. & LOVARI, S. (1996). — A review of wolf predation in Southern Europe - does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, 1561-1571.

PATALANO, M. & LOVARI, S. (1993). — Food habits and trophic niche overlap of the wolf *Canis lupus* (L., 1758), and the red fox *Vulpes vulpes* (L., 1758) in a Mediterranean mountain area. *Revue d'Ecologie (Terre et vie)*, 48: 23-38.

PIMLOTT, D.H. (1967). — Wolf predation and ungulate populations. *American Zoologist*, 7: 267-278.

PIMLOTT, D.H. (1975). — The ecology of wolf in North America, pp. 280-285. *In*: Fox, M.W. (ed.), *The wild canids: their systematic, behavioural ecology and evolution.* Van Nostrand-Reinhold, New York.

POTVIN, F. & JOLICŒUR, H. (1988). — Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Canadian Journal of Zoology*, 66: 1274-1279.

POULLE, M.-L., HOUARD, T. & DAHIER, T. (1995). — Le suivi des loups dans le Parc national du Mercantour. *Bulletin mensuel de l'Office National de la Chasse*, 201 : 36-45.

RAGNI, B., MARIANI, A., INVERNI, F. & MAGRINI, M. (1985). — Il lupo in Umbria, pp. 22-36. *In*: Boscagli G. (ed.), *Atti del Convegno Nazionale Gruppo Lupo Italia*. Gruppo lupo Italia, Pescasseroli, Italy.

REIG, S., CUESTA (DE LA), L. & PALACIOS, F. (1985). — The impact of human activities on the food of red fox and wolf in old Castille, Spain. *Revue d'Écologie (Terre et Vie)*, 40:151-155.

REIG, S. & JEDRZEJEWSKI, W. (1988). — Winter and early spring food of some carnivores in the Bialowieza National Park, eastern Poland. *Acta Theriologica*, 33: 57-65.

REYNOLDS, J.C. & AEBISCHER, N.J. (1991). — Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on the study of the fox, *Vulpes vulpes. Mammal Review*, 21: 97-122.

SALVADOR, A. & ABAD, P.L. (1987). — Food habits of a wolf population (*Canis lupus*) in León province, Spain. *Mammalia*, 51: 45-52.

TELLERÍA, J.L. & SÁEZ-ROYUELA, C. (1989). — Ecología de una poblacíon ibérica de lobos (*Canis lupus*). *Doñana, Acta Vertebrata*, 16: 105-122.

TEERINK, B.J. (1991). — *Hairs of west European mammals.* Cambridge University Press, Great Britain.

VIGNON, V. (1995). — Analyse de la prédation des ongulés par les loups (*Canis lupus*) dans un massif des monts cantabriques (Asturies, Espagne). *Cahiers d'Éthologie*, 15 : 81-92.